THE TYPE MATERIAL OF THE JURASSIC CEPHALOPOD *BELEMNOTHEUTIS*

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ABSTRACT. The coleoid genus *Belemnotheutis* Pearce, 1842, from the Lower Oxford Clay (Jurassic; Callovian) of Christian Malford, Wiltshire, England, gave rise to controversy and bad feeling between Richard Owen and Joseph Pearce, Gideon Mantell and others. Owen erroneously combined *Belemnotheutis* with an ordinary belemnite rostrum in his reconstructions of the belemnite animal. The type material of the type species, *B. antiquus* Pearce, is catalogued and described in detail for the first time. The species possessed a phragmocone with about 50 chambers, a muscular mantle, an ink sac, and ten arms furnished with pairs of hooks and also bearing suckers. Specimens range from about 100 mm to 300 mm in total length.

THE coleoid genus *Belemnotheutis* was described and named by Joseph Chaning Pearce (1811–1847) in 1842. It soon became the subject of acrimonious controversy between Richard Owen (1804–1892) on the one hand, and Pearce and his friends on the other. The present contribution gives a summary of the controversy, from published and unpublished material, and redescribes the type material.

HISTORICAL

The famous Oxford Clay locality of Christian Malford was discovered about 1840 during the construction of the Great Western Railway. Pearce heard of the finds in April, 1841 (Pearce 1842, p. 592; where the reference to Cheltenham must surely be a mistake for Chippenham) and visited the locality in the summer of the same year. The fossil cephalopods included ammonites with apertural features preserved and several kinds of coleoids. Fossils were collected and sold by dealers, but Pearce evidently collected his own material. He wrote to Owen (Appendix 1 (1)) on 18 March 1842 '... I remember your kindness when in London and since that period have been collecting... the Ammonites... from the Oxford Clay of Christian Malford to the extent of some hundreds of specimens...'. We cannot know the extent to which he also relied on professional collectors and/or exchange with others for material from this locality. Coleoids were rarer than ammonites and required careful excavation of the clays. Collectors or dealers kept the pit open until at least 1854 (Donovan 1983, p. 485). Dealers sometimes combined more than one imperfect fossil in order to produce a more 'complete' specimen (Donovan 1977, p. 31) and specimens in old collections must always be regarded with this possibility in mind.

Pearce read a paper on his finds to the Geological Society of London on 5 January 1842, published as an unillustrated abstract (Pearce 1842). The full paper was never published, perhaps because the ammonites with 'mouth-parts' which he mentioned had already been described and illustrated by Pratt (1841*a*) (see below). Among the fossils described by Pearce were 'remains of an animal considered to have been probably allied to a Sepia', belemnites, and 'an animal to which he has applied (since the paper was read) the name of Belemnotheutis'. The report of Pearce's description of this latter fossil was brief:

> '... the lower part is conical, blunt at the apex, and chambered internally like the alveolus of a Belemnite, with an oval siphunculus near the edge of the chambers... it has a brown thick shelly covering which gradually becomes thinner towards the superior part... immediately above the chambers is an ink-bag resting on what resembles the upper part of a sepiostaire, and composed of a yellow substance finely striated transversely, being formed

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> of laminae of unequal density... in some specimens, broken longitudinally through the middle, are exposed long, flat, narrow processes of a different structure... immediately beneath the superior contraction are two long feather-like processes, and one or more which are short, indicating, the author thinks, probably the situation of the mouth.'

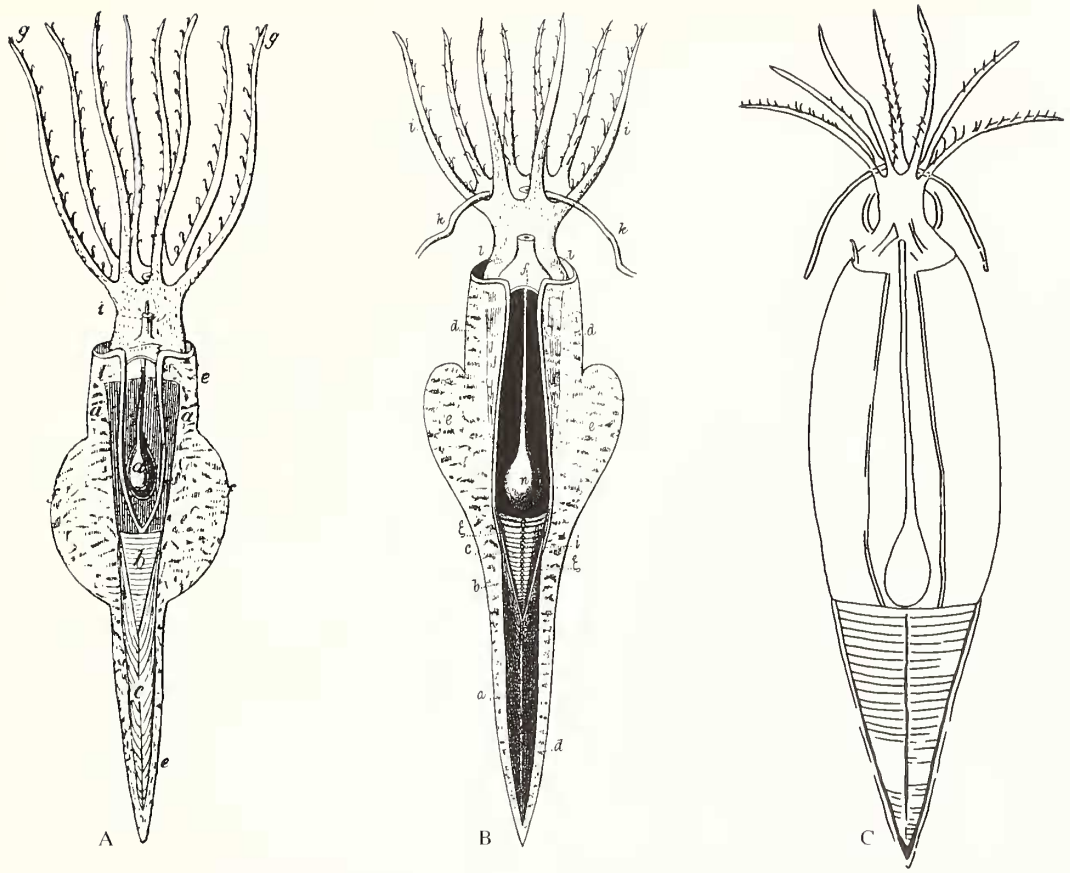
Richard Owen, who had described the first *Nautilus* to be brought to Europe in 1832, and had written the article on Cephalopoda for Rees' *Cyclopedia*, was present at the meeting (Pearce 1847, pp. 75–76). A year later his wife Caroline noted in her journal for 25 February 1843 'Mr. Pratt, the collector of belemnites, here. A most interesting collection of portions of this long mis-known fossil now in R's possession. The ink-bags, the striated portions of mantle, and tentacles with hooks, all beautifully clear.' (R. S. Owen 1894, **1**, p. 212). These remarks suggest that Owen had already made up his mind that the new Christian Malford fossils were belemnites. Shortly afterwards he exhibited a specimen obtained by the Marquis of Northampton (Owen 1844, pl. 3 or pl. 5) and one of the Pratt examples (Owen 1844, pl. 4) at the Hunterian Lectures at the Royal College of Surgeons, and in the published version of the lectures there is a reconstruction of a belemnite in which the characters of *Belemnotheutis* are combined with a belemnite guard (Owen 1843, p. 333, fig. 133) (Text-fig. 1A).

Samuel Peace Pratt F.R.S. (1789–1863) is credited with being the first to describe the exceptionally well-preserved ammonites from Christian Malford (Pratt 1841). The ammonites figured in his paper were chiefly specimens in the Bristol Institution collected by Samuel Stutchbury, the curator, and drawn by Stutchbury's assistant W. H. Baily. The majority are now in Bristol Museum. Pratt was induced to present some, at least, of his *Belemnotheutis* material (Owen 1856, specimen nos 25, 28, 30) to the Royal College of Surgeons, London, of which Owen was Conservator. Other specimens were presented to the College by the Marquis of Northampton P.R.S. (Owen 1856, specimen nos 26, 27, 29, 31, 32) and by W. J. Broderip F.R.S. (Owen 1844, p. 65), although the latter were not catalogued as *Belemnotheutis* by Owen (1856). All this material was unfortunately destroyed when the College was damaged during an air raid in 1941.

The fossils mentioned in the last paragraph were described by Owen in a paper read to the Royal Society on 21 and 28 March 1844 (Appendix 1, (2)), which was refereed by J. E. Gray (1800–1875) of the British Museum (Appendix 1, (3)), and published the same year (Owen 1844). A summary by D. T. Ansted was published by the Geological Society in February 1845 (Owen 1845). Owen made no mention of Pearce's prior paper to the Geological Society, or of his new name *Belemnotheutis*. He included the specimens to which Pearce had applied his name in the genus *Belemnites* and in the species *B. owenii* Pratt. Owen wrote (1844, p. 66) 'the species of Belemnite have been classified according to the modifications of the spathose guard; the one under consideration... was first recognised as a new species by Mr. Pratt, who has honoured me by naming it *Belemnites Owenii*'. This was in fact the first publication of the name (Sherborn 1929, p. 4662).

Owen believed that *Belemnotheutis* phragmocones had become detached from guards before fossilization, and that all such phragmocones had been associated, in life, with a belemnite guard of the common type. He wrote (1844, p. 70): 'The entire phragmocone, with its capsule [i.e. the aragonitic sheath], of these Belemnites from the Oxford clay, has been found not unfrequently isolated and detached, having slipt out of the alveolar cavity of the guard'. Except for this error, Owen gave a detailed and perceptive account of the Christian Malford *Belemnotheutis* and was probably the first to recognize fossilized muscular mantle, giving magnified pictures of the muscle fibres in *Belemnotheutis* and a modern squid (Owen 1844, pl. 7, figs 3–4). He used the presence of an ink sac to infer relationship with the living 'naked Cephalopods' and to classify the belemnites with his Dibranchiata as opposed to the *Nautilus* and the ammonites, in which ink sacs had never been found (Owen 1844, p. 72).

The restoration published by Owen (1844, pl. 8) was similar to that of 1843, with certain details added on the basis of a specimen lent by William Cunnington (now BM(NH) C.5020; Owen 1844, pl. 6). Owen thought that this showed parts of the tentacles, which he added to the restoration (Text-fig. 1B, *k*, *k*). It is one of a few specimens which have symmetrical semicircular structures on either



TEXT-FIG. 1. Reconstructions of belemnites and *Belemnotheutis* by Owen and Pearce. A, 'Belemnite restored' from Owen, 1843, p. 598. The rostrum *c* and phragmocone *b* are those of a typical belemnite. The arms with hooks and ink sac are based on *Belemnotheutis*, on account of Owen's erroneous assumption that the *Belemnotheutis* phragmocone had become separated from a belemnite guard. B, reconstruction from Owen, 1844, plate 8. Essentially the same as the 1843 restoration, except that a pair of tentacles *k* has been added. C, MS restoration by Pearce, date unknown, Bristol Museum archives, re-drawn by Colin Stuart.

side of the 'head'. Owen concluded (1844, p. 80) that these were the crystalline lenses of the eyes (Text-fig. 1B, *l*, *l*). They appear, however to be strips of muscular tissue.

Pearce made a reconstruction which was not published but survives in his papers (Appendix 1, (4)) and is here reproduced as Text-figure 1C. It appears to have been influenced by Owen's 1844 reconstruction (which Pearce had seen, see below) because of the way that the mantle is cut away to show the ink sac, and because tentacles are present. The correct *Belemnotheutis* phragmocone is of course shown and the semicircular structures are placed differently. Mantell published a reconstruction (1848, pl. 14, fig. 1) which shows the correct phragmocone, and lateral fins and tentacles following Owen's second version.

Owen evidently sent a copy of his 1844 paper to Chaning Pearce, who wrote to Owen in a letter dated 16 November 1844 (Appendix 1, (5)):

> 'It has given me great pleasure to read your paper on Belemnites from Christian Malford which you so kindly gave me but I think time will prove that the specimens with hooks belong to a distinct animal without a guard beyond the brown coating which invariably covers the chambers of this singular fossil. I examined this brown covering by Mr.

> Bowerbanks glass and he was decidedly of opinion that it was an external surface; you are aware no doubt, I described it as a distinct Genus (Belemnotheutis) some time ago in The Proceedings of the Geological Society and I am sorry you did not allude to it.'

Owen must have immediately written to James Scott Bowerbank (1797–1877) about the assertion that the brown coating of the phragmocone was an external surface, for Bowerbank replies to Owen on 20 November 1844 (Appendix 1 (6)):

> 'We *have* got so far as to be able to pronounce decidedly with the microscope whether a substance be corneous or membranous & that the substance under consideration is neither the one nor the other but composed of prismatic structure radiating from a line passing longitudinally through the body of the Animal & similar in appearance & structure to the bony substance of the Belemnite & this I shall be happy to demonstrate to you upon my own specimens whenever it may be convenient to you to come to my house to see it.'

Bowerbank then wrote of his intention to call at the Royal College of Surgeons in the hope of seeing Owen. They presumably met and discussed Pearce's letter, quoted above, for Bowerbank wrote to Pearce on 2 December (Appendix 1, (7)), with reference to the question of the external surface:

> '... I do not recollect the precise words I used but the import of them I well remember & which is: that the substance surrounding the Phragmacones was not "part & parcel" of the chambered portion or phragmacone but in reality equivalent to the solid fusiform belemnite & that it really represented that structure although in a very abbreviated form.'

He went on to say that he had again carefully examined the material and found that its structure agreed exactly with that of the belemnite guard, being composed of polygonal prismatic crystals, and that he had confirmed his original idea that the *Belemnotheutis* specimens

> 'are in fact neither *more* nor *less* than Belemnites having the spathose guard very much abbreviated, & this extreme shortness no more warrants us in separating it from the Genus Belemnites than the extreme length of B tubularis of the Lias would warrant us in making *it* the type of a New Genus.'

The conclusion that the sheath investing the phragmocone was homologous with the belemnite guard implied, of course, that Owen was wrong in believing that the *Belemnotheutis* phragmocones had become separated from normal belemnite guards. Bowerbank did not say so in so many words, but did write that 'Mr Owen is in error in making the one with the long spathose guard [*B. owenii*] ... to be the same species ...,' remarking that he had seen many belemnites with part of the phragmocone, but never one with part of the body preserved, and conversely none of the ones with the body *Belemnotheutis* had a 'long spathose guard'. Thus Bowerbank agreed with Pearce on the technical points but did not support *Belemnotheutis* as a separate genus.

In November 1846 Owen was awarded the Royal Society's Royal Medal in recognition of his 1844 paper on belemnites. The September 1846 number of a new (and short-lived) periodical, the *London Geological Journal*, included (without explanation) a copy of Owen's second reconstruction of the belemnite animal (Owen 1844, pl. 8). This prompted Pearce to send the editor a paper stating 'the facts which appear to me to oppose the conclusion, that these Cephalopoda [i.e. *Belemnotheutis*] are really the animals belonging to the well-known fossil bodies termed Belemnites' (Pearce 1847, p. 75).

The editor, Edward Charlesworth (1813–1893), printed the article in his February 1847 number, together with extracts from Owen's 1844 memoir, and an editorial in which he accused Owen of deliberately omitting from that memoir any mention of Pearce, his material or his study of it. He went on (Charlesworth 1847*a*, p. 81):

> 'We should not have thought this omission on the part of Prof. Owen required any special notice beyond the reference made to it by Mr. Pearce, were it not that like cases are so common as to constitute an evil of no slight magnitude in the progress of scientific research.'

He gave other examples where he considered that progress had been hindered by uncritical acceptance of the opinions of eminent authorities or the neglect of the views of less well-known

workers, discussing the influence of Deshayes and Agassiz at some length, and finally returning to his original point (Charlesworth 1847*a*, p. 85):

> 'Mr. Pearce may have no pretension to compete with Prof. Owen in a knowledge of the organic laws of the Cephalopoda, still his sagacity may be equal to the task of comparing the shell of Belemnoteuthis with the phragmocone of the Belemnite-guard, and judging how far the amount of correspondence admits the hypothesis of their being one and the same.'

Pearce's paper states and expands the microscopic evidence which had been supplied by Bowerbank and which has already been quoted, and emphasizes again that *Belemnotheutis* had never been found with a belemnite guard attached. The paper was illustrated by lithographs of two examples which Pearce had acquired since reading his 1842 paper [BRSMG Ca5242, Ca5240]. The generic name was now spelt *Belemnoteuthis*. The question of the correct form is discussed below (p. 280). The specific name *B. antiqnus* was introduced for the first time, presumably to bring home the fact that the fossils were not *Belemnites owenii* and perhaps also to ensure their separate identity even if the genus *Belemnotheutis* should be generally rejected.

Joseph Chaning Pearce took no further part in the controversy, for he died at Montague House, Lambridge, near Bath, on 11 May 1847. After his death (Appendix 1, (8)) the *London Geological Journal* published a note (Cunnington 1847) from William Cunnington (1813–1906), a well-known Wiltshire fossil collector, who supported Pearce's claim that Owen's restoration was a composite animal, but agreed with Bowerbank that the sheath or capsule of *Belemnotheutis* was the equivalent of the belemnite guard, and that *Belemnotheutis* was, therefore, not really a distinct genus. He noted the constant presence of two (dorsal) ridges (Owen had thought these were due to crushing of the fossil) and pointed out that they could not have fitted into the circular alveolus of the belemnite. Charlesworth, in an editorial dated 25 May, returned briefly to the subject and recorded that he had just seen new material found by Reginald Mantell near Trowbridge, in which the two ridges were clearly displayed (and, by implication, not artefacts of fossilization) (Charlesworth 1847*b*).

Reginald Neville Mantell, the engineer responsible for building a branch line of the Great Western Railway from Chippenham to Trowbridge, was the son of Gideon A. Mantell (1790–1852). A cutting at Trowbridge exposed the same beds as at Christian Malford, and a section through them was recorded for the first time (R. N. Mantell 1850). G. A. Mantell read a paper on his son's finds at the Royal Society on 23 March 1848 in which he upheld the distinction between ordinary belemnites and *Belemnotheutis*, emphasizing that the phragmocone of *Belemnothentis* could not have fitted into the alveolus of a belemnite guard. He had written to Owen expressing the hope that Owen would be present, 'to amend or corroborate my statements' (Appendix 1, (9)). However, as Mantell noted in his journal (G. A. Mantell, ed. Curwen 1940, p. 221):

> 'Royal Society – my paper on Belemnites read. Professor Owen made a most virulent attack on me, ridiculing the communication, and stating it was only fit for a few lines in the "Annals of Natural History". The Dean of Westminster [William Buckland] corroborated my views, and defended all my statements. The Marquess of Northampton [Spencer Joshua Alwyne Compton, 2nd Marquess] passed a warm eulogium ... to which the meeting which was a full one responded.'

Mantell gave another account of the meeting in a letter to the American geologist Benjamin Silliman (Spokes 1927, pp. 205–206). Charlesworth was also present and five weeks later he wrote from York to James Pearce, Joseph Chaning's father (Appendix 1, (10)):

> '[I]... felt glad that I had returned the *Belemnoteuthis* ... a drawing and description of it will be embodied in a Memoir of Dr. Mantell's which is to appear in the Transactions of the Royal Society. This Memoir was read at a late meeting of the Society and followed by a most animated discussion in which all who took part (including Buckland, Bowerbank & others) made a resolute stand against Owen on behalf of poor Chaning's Genus *Belemnoteuthis*. I longed as you may easily imagine to raise my voice in the cause, but not being an F.R.S. I could only have spoken by courtesy, and having so freely used the *Pen*, I thought under all the circumstances it was as well for me to be silent.'

Owen's behaviour at this meeting was the start of a feud between him and Gideon Mantell which

lasted until the latter's death. It led in turn to misunderstanding and bitterness, among other things about an Elgin reptile, *Leptopleuron* (Benton 1982). Owen had earlier approved of Mantell's geological achievements. In his lectures at the Royal College of Surgeons in 1843 he had said (Owen 1843, p. 5):

> '... the young provincial surgeon may be assured by the example of GIDEON MANTELL, that the researches and discoveries in palaeontology and geology, which have added so many honourable titles to that name, are quite compatible with the most extensive, active, and successful practice.'

Mantell's paper was refereed by Charles Lyell and Edward Forbes, who reported (Appendix 1, (11)):

> '... We recommend it to be printed in the Philosophical Transactions. In doing so, we neither assent nor dissent from the statements & reasoning therein contained & which are in opposition to those published in the Philosophical Transactions by another distinguished naturalist. As in each case the inferences have been duly considered by the respective authors, we think it desirable that both views of the organic remains in question should be contained in the same publication.'

The paper was duly published about June 1848.

In July 1849 Mantell wrote (Appendix 1, (12)) to Lyell, 'As to the distinct generic characters of Belemnite & Belemnoteuthis, no one now (except the great O) disputes it.' Later the same year, Owen opposed a move to award the Royal Society's Royal Medal to Mantell, who wrote in his journal (G. A. Mantell ed. Curwen 1940, p. 246):

> '(25 November) Professor Owen has done everything in his power to prevent me obtaining it! [the Royal Medal] What a pity that a man of so much talent and acquirement should be so dastardly and envious. (26 November) Professor Owen ... [claimed] ... my papers in the Transactions were unworthy such an honour! though he received it for his paper on the Belemnite, which has proved to be utterly erroneous.'

Mantell was awarded the Medal for his work on the *Iguanadon*, largely due to the support of Charles Lyell who was on the Council of the Royal Society (G. A. Mantell ed. Curwen 1940, pp. 246–247).

Early in 1850, on 14 February, Mantell read a supplementary paper to the Royal Society, in which he recorded 'uncompressed examples of the distal end of the phragmocones [of *Belemnotheutis*] which must dispel any remaining doubts as to the generic distinction ... being based on natural characters' (G. A. Mantell 1850, p. 395, pl. 29, fig. 7). He also figured (pl. 29, figs 9–10) broken apical ends of two phragmocones which showed that the thin layer enveloping the phragmocone possessed radiating fibrous structure and was thus equivalent to the rostrum or guard of ordinary belemnites.

In 1851, Mantell published his *Petrifactions and their teachings; or, a handbook to the gallery of organic remains of the British Museum* in which he wrote that the *Belemnotheutis* on exhibition '... incontrovertibly prove the correctness of the late Mr. Channing Pearce's opinion, that the soft parts of Cephalopoda found in the Oxford Clay, belong to a genus altogether distinct from the Belemnites with which they are associated' (G. A. Mantell 1851, p. 415) and gave a description of the genus. Referring to Owen's mistaken view, he added in a footnote (G. A. Mantell 1851, p. 460):

> 'I most studiously endeavoured to avoid giving offence to the eminant anatomist ... whose scientific labours I have so highly eulogized, and have done everything in my power to promote, by placing at his disposal original drawings ... and hundreds of specimens collected by my son; but alas! to doubt Professor Owen's infallibility was a deadly sin, and I have no hope of forgiveness!'

Hostilities continued. In March 1852 the *Quarterly Review* carried an unsigned article with the running head 'Progress of comparative anatomy' (Anon. 1852), a fulsome review in which Owen's position on the belemnite question was still asserted to be the correct one. The article was in fact written by Owen's patron, W. J. Broderip (1789–1859) and the proofs corrected by Owen himself

(A. J. Desmond, pers. comm.). Mantell responded (Mantell 1852) and Broderip (or Owen?) replied in turn (Quarterly Reviewer 1852).

John Morris in the second edition of his *British Fossils* (Morris 1854) accepted Pearce's species *antiquus*, though he gave the wrong reference for it (Pearce 1842) and regarded *Belemnotheutis* as a generic synonym of *Acanthoteuthis* Wagner, 1938, which had been set up for hook-bearing arm crowns from the Lithographic Limestone (Upper Jurassic) of Solnhofen, Germany.

Owen, though he never publicly withdrew his criticism of Pearce and of Mantell, did in fact change his mind. In 1855, in the second edition of his lectures on invertebrates he referred to 'apparently guardless species' (Owen 1855, p. 603, footnote) though he reproduced (fig. 218, p. 598) the erroneous restoration from his 1843 edition. In 1856 was published the '*Descriptive Catalogue* ...' of invertebrate fossils in the Museum of the Royal College of Surgeons of London, cephalopod entries being by Owen (Owen 1856, p. vi), who now followed Morris in accepting *Acanthoteuthis* with *Belemnoteuthis* [*sic*] as a synonym. After mentioning 'the supposition of its having slipped, like No. 13 [a belemnite] from the alveolus of a belemnitic guard of the ordinary structure' he wrote (Owen 1856, p. 1):

> '... but, as it appears that the corneo-calcareous capsule is somewhat thicker than in the phragmocone *in situ*, and as several crushed and apparently detached or unguarded phragmocones ... have been discovered in the same formation, a second hypothesis has been propounded, viz. that they have been originally uncomplicated by the normal belemnitic spathose guard, and that they represent a distinct genus or subgenus of the extinct *Belemnitidae*, for which the names *Acanthoteuthis* and *Belemnoteuthis* have been proposed, and in the present instance with the specific name of *antiquus*.'

Finally, in his *Palaeontology* (1860, p. 92, fig. 22) Owen illustrated as separate species *Belemnites Oweni*, a guard and phragmocone, and *Acanthoteuthis antiquus* exemplified by a Christian Malford specimen in the British Museum (no. 25966) which was later refigured by Donovan (1977, fig. 6). Owen attributed the species *antiquus* to Cunnington. He was explicit, at last, as to his own change of opinion (Owen 1860, pp. 91–92):

> '... further evidence ... has been supplied by the Chippenham fossils, which in all probability are identical in genus, if not in species, with the *Acanthoteuthis* described by Muenster. One of these extraordinary fossils ... is represented in (fig. 22, 2) ... [here follows a description] ... This shell, which is chambered internally, [p. 92] like the *phragmocone* of the Belemnite (fig. 22, 1), has an outer sheath of fibrous structure, one-fourth of an inch thick at the apex, and furnished with two converging ridges on its dorsal side; the external surface, however, is horny (or chitinous), like the pen of the Calamary. These chambered shells occur in great numbers, and are so like the phragmocones of the associated Belemnites, both in structure and proportions, that they were originally described by me as such, and I still view them as evidences of the close affinity of the cephalopod possessing them to the true Belemnite: ...'.

This came too late, unfortunately, to do justice to Pearce, or to Mantell who had died on 10 November 1852.

History of the Pearce Collection

The fossil collection of J. Chaning Pearce (1811–1847) remained in the possession of his son until 1 November 1915 when it was bought for £1000 and given to Bristol City Museum. It was kept in store and so escaped the destruction of the greater part of the Museum's geological collection in an air raid in November 1940. The collection includes the material on which Pearce based his genus *Belemnotheutis*, now fully described for the first time. The collection is accompanied by Pearce's MS catalogue. The date of the entries is not known, but is later than the adoption of the spelling *Belemnoteuthis* (see below) some time after 1844. The relevant material is listed with notes on the catalogue entries in Appendix 2.

SYSTEMATIC PALAEONTOLOGY

Subclass COLEOIDEA Bather, 1888
Order BELEMNITIDA Zittel, 1895 (*nom. correct. pro* Belemnoidea)
Family BELEMNOTHEUTIDIDAE Zittel, 1884 (*nom. correct. pro* -teuthidae)
Genus BELEMNOTHEUTIS Pearce, 1842

Abbreviations. BM(NH), British Museum (Natural History), South Kensington, London SW7 5BD. BRSMG, City of Bristol Museums and Art Gallery, Queen's Road, Bristol BS8 1RL. Specimen registration numbers with the prefixes Ca, Cb and Cd are in the Bristol Museum and are listed below in Appendix 2.

Spelling of generic name. The generic name *Belemnotheutis* (*sic*) was first published in the *Proceedings of the Geological Society of London* in 1842 (Pearce 1842*a*, p. 593), in the report of a meeting at which Pearce had exhibited some fossils from the Oxford Clay of Christian Malford. It is spelt in the same way in the index to the volume. An unchanged copy of the report was published in the *Annals and Magazine of Natural History* (Pearce 1842*b*). Pearce (1847, p. 75, footnote) said that the name had been suggested by J. E. Gray, who later (1847, p. 206) used the spelling *Belemniteuthis*, probably inadvertently. Owen (1855, p. 602, footnote), more improbably in view of the history given above, also claimed paternity. No species name was mentioned in the 1842 report.

Pearce's paper (1842*a*) was reported in the *Neues Jahrbuch* (Pearce 1843) with the spelling *Belemnoteuthis*. Agassiz ([1845], p. 11) also used this form, and was presumed by Sherborn (1924, p. 681) to have emended the spelling. However, we do not know whether the change of spelling in the *Neues Jahrbuch* and in Agassiz ([1845]) was intentional or a mis-reading for the more familiar *-teuthis*. Although Pearce's original spelling was correctly listed by Sherborn (1924, p. 681) and Neave (1939, p. 413), authors have continued to use the form *Belemnoteuthis*.

If the emendation was intentional it is not justified under the Rules of Zoological Nomenclature now in force. The matter is covered by Article 32(c) 'Incorrect original spelling'. An original spelling is there deemed to be incorrect if (i) it contravenes a provision of Articles 27–31 (which deal with such matters as gender, capitalization, diacritic marks and family-group endings), or (ii) there is clear evidence in the original publication of an error such as a copyist's or printer's error. It is explicitly stated that 'Incorrect transliteration or latinization ... are not to be considered inadvertent errors'. Unless an original spelling is incorrect by these criteria, the original spelling is to be preserved.

The form *Belemnotheutis* appears on some of Pearce's MS specimen labels, corrected to *Belemnoteuthis*. Pearce also used the spelling *-theutis* in letters to Owen dated 16 November 1844 and 18 December 1844. This form was therefore used by Pearce at least up to 1844 and was not a scribe's error or a misprint in the Geological Society's *Proceedings*.

We do not know why Pearce used this spelling. We are informed (Alan Griffiths, pers. comm.) that *teuthis* (Gr. τευθίς) is the usual form, but that the form *-theutis* (Gr. θευγίς) is recorded once by an Ionic writer. In fact, the form *-theutis* is also used on MS labels dating from the mid-nineteenth century in the Staatliches Museum für Naturkunde, Stuttgart, e.g. *Geotheutis* instead of *Geoteuthis*, and endings such as *-theutis*, *-theusis* and other variants are found for other coleoid genera in nineteenth-century authors. There appears, therefore, to have been equivocation as to the correct form.

We conclude, that whatever the reason for the original spelling, it was intended, and that emendation to *Belemnoteuthis* is not justified by the Rules now in force.

Type species. Pearce's 1847 paper in the *London Geological Journal* was illustrated by two plates (15 and 16) showing specimens now in the Pearce collection at Bristol. Each plate bears the name *Belemnoteuthis antiquus* Pearce, although the specific name does not appear in the text. This was the first publication of the combination *Belemnoteuthis antiquus*. No other species is mentioned. We conclude that the species *Belemnotheutis antiquus* Pearce, 1847 is the type species of *Belemnotheutis* Pearce, 1842 by monotypy (Article 68(d)).

EXPLANATION OF PLATE 1

Belemnotheutis antiquus Pearce. BRSMG Ca5240, lectotype, Pearce Collection; dorsal view, ×0·75. (Previously figured by Pearce (1847, pl. 16); for enlarged details see Plate 2.)

Systematic position. Belemnotheutis is here included in the Order Belemnitida following Jeletzky (1966, pp. 145–146), Bandel and Kulicki (1988, p. 315) and Peter Doyle (pers. comm. 1990), and in disagreement with the view expressed by Donovan (1977, p. 29). The principal reason for doubt by Donovan (1977) was the aragonitic rostrum of *Belemnotheutis antiquus* compared with the apparently calcitic one of typical belemnites. More recently it appears that the epirostrum of certain belemnites may be aragonitic (Bandel and Spaeth 1988), so that this distinction loses its force.

Relationship to Acanthoteuthis. The genus *Acanthoteuthis* was proposed by Wagner (1839, p. 94) for coleoids with hooked arms from the Lithographic Limestone (Solnhofener Plattenkalk) of the Solnhofen area, Bavaria. Naef (1922, pp. 180, 252, fig. 91) showed that there were ten arms of approximately equal length. Later finds (e.g. Engeser and Reitner 1981, fig. 5) show that these arm crowns belonged to animals with a shell like that of *Belemnotheutis antiquus*. The chief differences lie in the narrower apical angle of the phragmocone, about 13° (uncrushed), fewer septa (between 40 and 45), and a relatively longer pro-ostracum. The arm hooks are similar to those of *Belemnotheutis antiquus*.

As already noted, early authors (Morris 1854; Owen 1856) regarded *Belemnotheutis* as a synonym of the prior *Acanthoteuthis*. Zittel (1884) separated them but he erroneously regarded *Acanthoteuthis* as an octopod. Naef (1922, p. 186) noted the close similarity between the two genera, and kept them separate principally because of the presence of a well-developed 'Scheide' (lit. sheath; ? rostrum) in *Belemnotheutis*; this does not now seem to be a distinction. Engeser and Reitner (1981) kept them separate. It is at least arguable that the differences between the two forms are hardly of generic significance.

Stratigraphical range of Belemnotheutis. The earliest example is from the Kellaways Rock (Lower Callovian; *calloviense* Zone) of Wiltshire, England (BM(NH) 37440). *Belemnotheutis polonica* Makowski from Łuków, east of Warsaw, Poland, comes from a nodule bed of *lamberti* Zone (Upper Callovian) age (Arkell 1956, p. 482). Riegraf (1987) described a crushed phragmocone indistinguishable from that of *B. antiquus* from the Kimmeridge Clay of Kimmeridge Bay, Dorset, England. The exact horizon is not stated but the locality suggests the uppermost Lower, or early Upper Kimmeridge Clay, i.e. *pseudomutabilis* or *gigas* Zone. The youngest example is from the Upper Kimmeridge Clay (Upper Kimmeridgian Stage: ?*pallasioides* Zone) of Kimmeridge, Dorset (BM(NH) C.59184). Doyle (1991, p. 172) records a ?*Belemnotheutis* [phragmocone] from the Nordenskjöld Formation of the Antarctic Peninsula, Antarctica, which would be Upper Kimmeridgian in north European terms. The genus therefore ranges through the greater part of the Callovian, the Oxfordian, and most of the Kimmeridgian Stage. Engeser and Clarke (1988, pp. 137–138) note that the belemnotheutids possibly range up to the Upper Cretaceous on the evidence of '*Belemnoteuthis*' *syriaca* Roger, 1944.

Belemnotheutis antiquus Pearce, 1847

Plates 1–5; Text-figs 2–3

1844 *Belemnites Owenii*; Owen, pl. 2, figs 6–8; pl. 3; pl. 4, figs 1–2; pl. 5; pl. 6, figs 1–3; pl. 7, fig. 4 [*pars*, *non* Pratt *in* Owen].
1847 *Belemnoteuthis antiquus* Pearce, pls 15–16.
1848 *Belemnoteuthis antiquus* Pearce; Mantell, p. 172, pl. 13, figs 1–3, 5.
1850 *Belemnoteuthis* Mantell, p. 395, pl. 29, figs 7, 9–10.
1851 *Belemnoteuthis antiquus* Pearce; Mantell, p. 459, lign. 100.
1852 *Belemnoteuthis antiquus* [Pearce]; Mantell, p. 18, fig. 3.
1854 *Acanthoteuthis antiquus* Pearce; Morris, p. 289.
1856 *Acanthoteuthis* (*Belemnoteuthis*) *antiquus* Wagner and Pearce; Owen, p. 11.
1966 *Belemnoteuthis antiqua* Pearce; Jeletzky, p. 78, pl. 16, fig. 2.
1977 *Belemnoteuthis antiqua* Pearce; Donovan, p. 27, fig. 6.
1991 *Belemnotheutis antiquus* Pearce; Page *in* Martill and Hudson, p. 156, pl. 31, figs 2–3.

EXPLANATION OF PLATE 2

Figs 1–4. *Belemnotheutis antiquus* Pearce. BRSMG Ca5240, lectotype, Pearce Collection. 1, Arm crown, × 1·25. 2, Detail of hooks and suckers (detail of fig. 3), × 7·8. 3, Parts of two arms, × 4·85. 4, Detail of hooks and suckers, × 6·7.

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DONOVAN and CRANE, *Belemnotheutis*

Type series. The specific name was published in February 1847. Pearce died in May 1847 (see above), and the specimens listed as *Belemnoteuthis antiquus* in Pearce's MS catalogue which accompanies his collection in Bristol Museum are assumed to have been available when he wrote his 1847 paper and are therefore syntypes. They are listed and briefly described below (Appendix 2).

Lectotype. The original of Pearce (1847, pl. 16), Pearce no. 160A, now BRSMG no. Ca5240, is here designated the lectotype. It is here refigured (Pls 1–2) and described.

Paralectotypes. The syntypes other than the lectotype become paralectotypes (Article 73(b)(ii); Recommendation 74E). One of the specimens catalogued by Pearce as 160G (now BRSMG Cb3975) is here regarded as doubtfully belonging to the species.

Locality and horizon. All of Pearce's specimens were obtained from the Oxford Clay of Christian Malford in Wiltshire, England, exposed during railway construction about 1840. There is no detailed contemporary description of the occurrence, and the scanty information was summarized by Woodward (1985, p. 32), White (1925, p. 12) and Donovan (1983, p. 485). An approximate National Grid Reference is ST 960777. The zonal horizon is shown by the associated ammonites to be the *phaeinum* Subzone, *athleta* Zone of the Callovian Stage (Donovan 1983, pp. 486–487; Page *in* Martill and Hudson 1991, p. 156).

Mode of preservation. The *Belemnotheutis* specimens from Christian Malford are remarkable for the preservation of permineralized soft tissues. It is clear that the fossils were preserved in laminated, bituminous shales with an impoverished benthic fauna and little or no bioturbation. In addition to presumed pelagic fishes and cephalopods, Woodward (1895, p. 32) listed two genera of gastropods (including '*Patella*') and three species of bivalves, recorded as *Avicula ovalis*, *Leda phillipsi* and *Pholadomya deltoidea*. These did not necessarily come from the same horizon as the coleoids with permineralized soft parts.

Only the coleoids *Belemnotheutis* and *Mastigophora* (Donovan 1983) show permineralized soft tissues. In the case of *Belemnotheutis*, which possessed an aragonitic phragmocone, isolated phragmocones without associated soft tissue are perhaps five to ten times as numerous in collections as specimens with soft parts. This ratio is clearly an unsafe guide to their original abundance. We do not know, for example, whether the isolated phragmocones and the soft part specimens were found on the same or different bedding planes. Pearce (1842, p. 593) refers to 'four or five bands of laminated clay' but does not specify their fossil content in detail. Fragments of fish and of ammonites on slabs with *Belemnotheutis* soft parts do show that these fossils all occurred together. At Trowbridge, where R. N. Mantell later encountered the same, or a closely similar, horizon, phragmocones were common but well-preserved soft parts were not found (G. A. Mantell 1848, p. 173).

Allison (1988) studied the composition and structure of the fossilized soft parts and offered an interpretation of their preservation. The permineralized tissue is composed of apatite which under high SEM magnification resolves into spheres of 1–2 μm diameter. Allison suggested that the mineralization occurred near the oxic/anoxic boundary after the carcases sank rapidly into a 'soupy' surface layer of sediment. Mineralization was favoured by high pH but the chemical processes could not be exactly determined. The high pH would of course be consistent with the perfect preservation of the aragonite of the *Belemnotheutis* phragmocones and of the ammonite shells. Allison does not discuss why soft part preservation is not found in fossil groups other than coleoids which were found at Christian Malford.

Description of the lectotype. The phragmocone and rostrum together are 72 mm long and about 30 mm in maximum breadth. The anterior end of the phragmocone is cut off sharply due to preparation. The apical angle is about 36 degrees. The posterior end shows a deep, narrow groove, bounded by rounded ridges, dying out anteriorly. This shows that the specimen is seen from the dorsal side.

The 'body' is preserved as the muscular mantle which extends from about 62 mm forward of the apex of the phragmocone to about 179 mm from the same point. In places it shows transverse striations, 4 or 5 to the

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EXPLANATION OF PLATE 3

Figs 1–2. *Belemnotheutis antiquus* Pearce. Paralectotypes. 1, BRSMG Cd22*a*. Pearce Collection; anterior to phragmocone is hollow left by ink sac, flanked by probable fragments of pro-ostracum, × 1. 2, BRSMG Cd18*a*, Pearce Collection; dorsal view, × 1·25 (for details see Plate 4, fig. 2, and Plate 5).

1

2

DONOVAN and CRANE, *Belemnotheutis*

millimetre. The anterior end of the 'body' is sharp and is the result of preparation. No detail can be discerned in the 'body'. Near the front end several narrow strips, 1–2 mm wide, lie on the surface of the mantle.

There is a gap between the 'body' and the arm crown, due to preparation. There is no reason to suppose that the arm crown does not belong to the rest of the fossil. The positions of the arms are indicated by double rows of hooks, in some cases associated with suckers (Pl. 2, fig. 1).

There are at least seven arms, possibly more. The bases of the arms are vaguely defined and their exact length cannot be measured; it was probably more than 100 mm. There is nothing to indicate that different arms were of markedly different lengths. Where suckers are preserved there are the same number of pairs of hooks as suckers, but it is not clear whether the hooks are rooted in the suckers, as they sometimes appear to be (Pl. 2, fig. 2). There could have been only one row of suckers per arm. Distal suckers are smaller than proximal ones, the largest being about 2 mm in diameter. Several suckers show what could have been a chitinous ring around the outside (Pl. 2, fig. 4). Mantell (1852, p. 19, fig. 4) illustrated 'three hooks with attached horny rings; from a specimen in the possession of Mr. Cunnington', an interpretation which was doubted, for no apparent reason, by Engeser and Clarke (1988, p. 139). The specimen in question is not known to be extant.

Description of other material. Fossils from Christian Malford were widely distributed during the 1840s and 1850s through dealers and probably by exchange. The following account of *Belemnotheutis antiquus* is based on the Pearce material supplemented by that of the BM(NH) and of the Royal College of Surgeons (now lost) published by Owen (1844).

Phragmocone. Isolated phragmocones, almost all from the original Christian Malford locality, are relatively common in old collections. There are eight in the Pearce Collection and about 40 in the BM(NH). Most are crushed and thus visible in two dimensions only. The phragmocone was evidently conical; the transverse section was presumably circular or elliptical, but cannot be ascertained from the material. The angle of the cone at the apex, as measured on crushed specimens, ranges from about 27° to 36°, the mean being about 33° and the standard deviation about 2·42°, based on measurements of 25 well-preserved examples in the Pearce collection and the BM(NH). If conical phragmocones were completely flattened the average apical angle of the uncrushed phragmocones would have been about 21°. One example in which the apex is almost uncrushed (BM(NH) 21449) has an apical angle of 17·5°. In the crushed specimens there often appears to be an increase in the angle of the cone from the apex forwards, but this is probably an artefact caused by greater strength, and therefore less complete flattening, of the apical end.

The uncrushed phragmocone figured by Mantell (1850, pl. 29, fig. 7) has an apical angle of 18°. An uncrushed phragmocone in the Pearce collection (BRSMG Cb3976), preserved in non-laminated mudstone and not certainly belonging to *Belemnotheutis*, has an apical angle of 22°. The closely similar phragmocones from Poland, described by Makowski (1952) as *Belemnoteuthis polonica*, are uncrushed and have apical angles of 20° to 21°.

The overall length of 32 phragmocones measured ranges from 35 to 86 mm. The mean is about 64 mm, but the mode is higher, in the 71 to 75 mm class, so that the distribution is skewed or possibly bimodal. An exceptionally large individual (BM(NH) 88603), not included in these measurements, has a phragmocone around 100 mm long. An even larger specimen in the Pearce Collection (BRSMG Cb3972) appears to be about 300 mm long but is probably compounded of two individuals. Even so these are much larger than other phragmocones of *Belemnotheutis antiquus* and are here excluded from the species.

Chambers increase in length from about 0·5 to about 4·0 mm, measured as the distance between suture lines. Twenty measurements on 17 specimens yielded the relationship:

$$y = 0{\cdot}0516x - 0{\cdot}0755$$

where y is chamber length and x is distance to the chamber from the apex. There is a positive correlation coefficient of 0·975 between the two measurements. The total number of chambers cannot be counted in any specimen, but is estimated to have been about 50 in large (80 mm long) phragmocones.

EXPLANATION OF PLATE 4

Figs 1–2. *Belemnotheutis antiquus* Pearce. Paralectotypes. 1, BRSMG Cd22*b*, Pearce Collection; arm crown, ×1.09. (For detail of arm hooks see Text-fig. 3B.) 2, BRSMG Cd18*a*, Pearce Collection; detail of muscles of neck region, ×2·4. (Transversely striated mantle muscle is seen at the bottom of the figure; for whole fossil see Plate 3, fig. 2.)

1

2

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The siphuncle is not clearly seen in the type material, but the Polish material (Makowski 1952) shows it to have been marginal and ventral. The protoconch cannot be studied in the type material. Apparent differences in the protoconch of Polish material from that of typical belemnites (Donovan 1977, p. 27) have been explained as the result of shell damage during life (Bandel and Kulicki 1988).

Specimens for which the proportion of the phragmocone as part of the total length can be determined are few. They indicate that the phragmocone is about 0·30 of total length including arms.

Rostrum. The apical part of the phragmocone is covered by the rostrum, aragonitic in composition (Donovan, 1977, p. 28; Bandel and Kulicki 1988, p. 304), up to 1 mm thick at the apex in the largest specimens. The thickness diminishes anteriorly so that a little more than half way from the apex to the anterior margin the septal sutures become visible through the thin conotheca. The rostrum has a narrow mid-dorsal groove flanked by rounded ridges, ill-defined on their lateral sides (Pls 2, 5). The position of the groove cannot be determined in the type material, but in *B. polonica* it is mid-dorsal as shown by growth lines which indicate a pro-ostracum in the same position (Makowski 1952, text-figs 7–8). The groove is well marked apically and persists for up to 3/5ths of the length of the phragmocone. Initially angular in section, it becomes flat-bottomed, about 1 mm wide, with fine ribs before dying out. This detail can be seen in a few Christian Malford specimens (e.g. BM(NH) 30460, C.7854) but is better studied in uncrushed examples from the Kellaways Rock (BM(NH) 37440, C.46500–46501) and is well shown by Makowski's enlarged figures (1952, text-figs 7–8).

Owen regarded the paired ridges as accidental, due to crushing. They were correctly interpreted by Cunnington (1847), and by Mantell (1848, p. 175, pl. 14, fig. 4) who wrongly regarded them as ventral in position. Mantell also described and figured (1848, p. 175, pl. 14, fig. 3) a median dorsal (i.e. ventral) ridge but this does seem to have been an artefact of preservation. No such ridge is seen in the uncrushed material of *B. polonica* illustrated by Makowski (1952).

Pro-ostracum. The pro-ostracum is poorly known. The proximal part may be shown by BRSMG Cd16/17, and probable displaced fragments by Cd22*a* (Pl. 3, fig. 1). The junction of the pro-ostracum with the dorsal margin of the phragmocone is not seen in any specimen, but phragmocones BRSMG Cb3966 and BRSMG Cb3971 show faint oblique growth lines in the right-hand anterior region which appear to be part of a hyperbolar zone.

The length of the pro-ostracum was about 1·2 times the length of the phragmocone, according to the example from the Sedgwick Museum, Cambridge (J24841) figured by Jeletzky (1966, pl. 16, fig. 2). The width is difficult to establish but was substantially less than the width of the flattened phragmocone. There are slight indications that the lateral margins were thickened. If BRSMG Cd16 can be relied on, the pro-ostracum tapered weakly forwards. The Cambridge specimen figured by Jeletzky appears to have a semicircular front end, but growth lines on Makowski's *B. polonica* (1952, text-figs 7–9) show a bluntly pointed end and this is likely to have been so in *B. antiquus*. The pro-ostracum was non-calcareous but its composition has not been determined.

Body. The body of the animal consists chiefly of the muscular mantle, roughly parallel sided but varying in outline according to the amount of disturbance during fossilization, and also modified by preparation. If the body was cylindrical in life and has been perfectly flattened, then the original diameter would have been about 12–14% of the overall length. This estimate cannot be regarded as very reliable.

The muscular mantle is preserved in some specimens as a whitish layer less than 1 mm thick. It bears transverse striations about 0·20 to 0·25 mm apart (Pl. 3, figs 1–2; Pl. 5).

The ink sac lay within the mantle. Its position may be shown by a swelling as the fossilized ink was less compressible than the rest of the fossil (e.g. BRSMG Cd21, Text-fig. 2). In some specimens it has been exposed by the removal of the overlying mantle. The sac lies immediately in front of the phragmocone, and may be about 25 mm long in large individuals. The duct is two or three millimetres across and leads forward to a point near the front of the mantle.

One specimen (BRSMG Cd18*a–b*) shows a feature near the anterior end which Pearce in his MS Catalogue

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EXPLANATION OF PLATE 5

Belemnotheutis antiquus Pearce. Paralectotype, BRSMG Cd18*a*, Pearce Collection; phragmocone, dorsal view, ×2·6. (Transversely striated mantle muscle is visible at the top of the figure; for whole fossil see Plate 3, fig. 2.)

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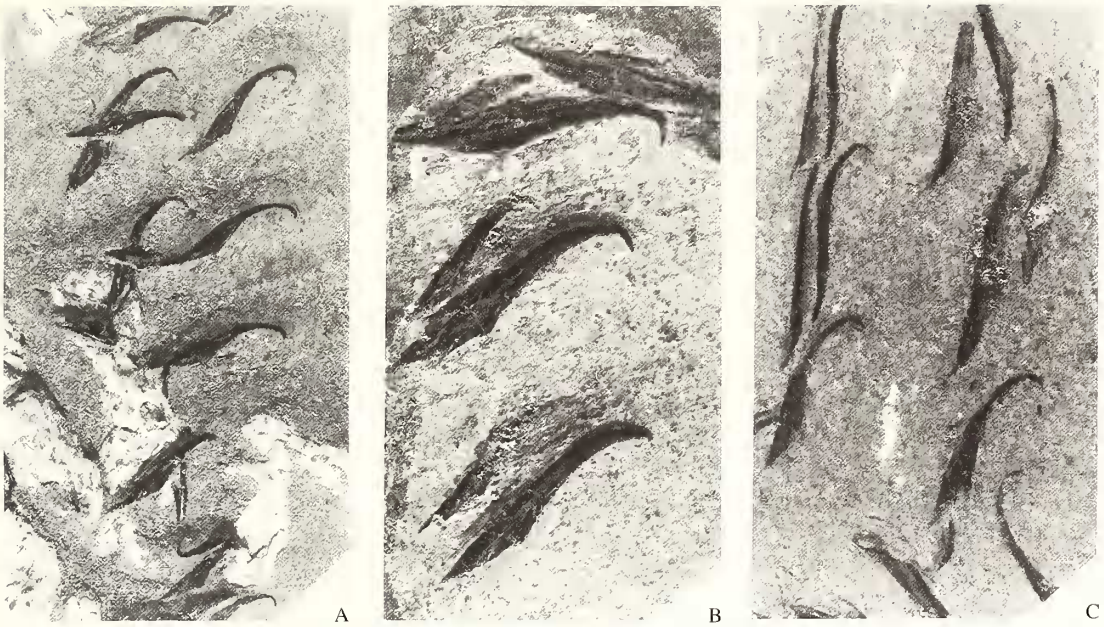
TEXT-FIG. 2. *Belemnotheutis antiquus* Pearce, BRSMG Cd21, paralectotype, Pearce Collection, × 1. The ink sac is visible as a swelling immediately in front of the anterior margin of the phragmocone. For detail of arm hooks see Text-figure 3c.



TEXT-FIG. 3. *Belemnotheutis antiquus* Pearce, paralectotypes. A, BRSMG Cb7661; detail of arm hooks and arm muscle, ×4. B, BRSMG Cd22B; detail of arm hooks, ×5·9; for whole arm crown see Plate 4, fig. 1. C, BRSMG Cd21; detail of arm hooks, ×5·8; for whole fossil see Text-figure 2.

described as 'feathery processes' (Pl. 3, fig. 2; Pl. 4, fig. 2). Examination with the binocular microscope and the SEM shows that this feature is in fact mineralized muscular tissue. It appears to be muscles of the dorsal neck region, and shows some similarity in arrangement to the dorsal neck muscles of the Recent coleoid *Vampyroteuthis* (Young 1964, pl. 5).

Head. The head is not clearly preserved in any of the Pearce specimens. Several BM(NH) specimens show a pair of semicircular strips of tissue, about 2–3 mm wide, on either side of the head (C.5020 figured by Owen 1844, pl. 6, figs 1–3; 25966 figured by Mantell 1851, fig. 100, p. 459; 88603, unfigured). The function of these structures is unknown.

Arms. The greatest number of arms preserved in any specimen (BM(NH) 25966; Donovan 1977, fig. 6) is nine. Assuming bilateral symmetry the original number is thought to have been ten. The arms vary in length according to the size of the individual, but their length is difficult to measure because they are often incompletely preserved, and their bases are usually obscure. They were probably more than 100 mm long in large specimens, about 40% of the total length of the animal including the arms. The arms may be preserved as soft tissue plus paired hooks (e.g. BRSMG Cd22*b*, Text-fig. 3B) or by hooks alone (e.g. BRSMG Cd21, Text-fig. 3C) showing varying degrees of disturbance from their original disposition. The soft tissue usually appears as a narrow strip two or three millimetres wide. Suckers have been described in the lectotype (above, p. 286).

There is some variation in shape of hooks, some appearing relatively narrower than others (e.g. Text-fig. 3C, left-hand side). This may be due to incomplete removal of matrix. Engeser and Clarke (1988) have discussed arm hooks in fossil and Recent coleoids. The form present in *Belemnotheutis* is found in several species until the late Cretaceous.

Size. As a measure of total size, it is not useful to measure 'mantle length' as with living coleoids. In most specimens the anterior and posterior limits of the mantle are ill-defined and have generally been modified by unskilled preparation. No clearly-defined head is distinguishable on any example. Total length of specimens has therefore been measured, but is of limited value because of the different configurations in which arms are preserved.

Examples which are more or less complete are rare. The smallest are some poorly preserved examples in the

BM(NH) (24678, 89182, C.2693) which are about 100–120 mm in overall length. Better preserved material ranges from about 135 mm (BM(NH) C.2692, BRSMG Ca5242) to about 250 mm (lectotype), and, exceptionally, about 300 mm (BM(NH) 88603). The ratio between lengths of smallest and largest is thus approximately 1:3, about the same as that between the extreme sizes of phragmocones.

Comparisons. Belemnotheutis polonica Makowski, 1952, from the Callovian of Poland, was based on well-preserved phragmocones and rostra only. No soft parts are known. Bandel and Kulicki (1988, p. 314) remark that it is difficult to separate this species from *B. antiquus*. *Belemnotheutis mayri* Engeser and Reitner, 1981, from the Solnhofener Plattenkalk (Lower Tithonian), has a phragmocone with a smaller apical angle than *B. antiquus*, and the arms form a much smaller proportion of the total length.

DISCUSSION

An extended discussion of the relationships of *Belemnotheutis* will not be attempted here, as this will be included in a forthcoming volume of the *Treatise on invertebrate paleontology* dealing with Coleoidea which is now in active preparation. However, it may be remarked that suckers were regarded by Berthold and Engeser (1987) as characteristic of Dibranchiata (in their sense) which exclude, and are treated as a sister group of, 'Belemnoidea'. The presence of suckers in *Belemnotheutis* shows that suckers are not autapomorphic for Dibranchiata *sensu* Berthold and Engeser. Suckers are known in at least two Jurassic teuthids: *Gramadella* (Fischer and Riou 1982) and *Mastigophora* (BM(NH) no. 32352, unpublished). Engeser and Clarke (1988), as mentioned above, have argued convincingly that the arm hooks present in some Recent squids evolved independently of those found in Mesozoic coleoids. However, it is likely that suckers were already present in the common ancestors of the Belemnitida and the living forms.

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APPENDIX 1

Archival sources for the historical part of the paper

(1) Letter from Pearce to Richard Owen dated 18 March 1842. BM(NH) Owen Correspondence xxi, 187–8.
(2) Journal Book of the Royal Society XLIX, 1843–1859. The drawings to illustrate the paper are filed at PT.75.53–8.
(3) Gray's report on the paper is filed by the Royal Society at MC 4.20.
(4) BRSMG, Geology File PEA 5.
(5) Letter dated 16 November 1844 from Pearce at Bradford [-on-Avon], Wiltshire, to Richard Owen. BM(NH) Owen Correspondence, xxi, 197–198. Photocopy in BRSMG Geology File PEA 7.
(6) BM(NH) Owen Correspondence, iv, 322–323. Photocopy in BRSMG Geology File PEA 17.
(7) BRSMG, Geology File PEA 2.

(8) No. 3 of the *London Geological Journal*, for May 1847, printed a letter on the back cover dated 22 June 1847 and could not have been issued before that date.
(9) Mantell to Owen 23 March 1848, BM(NH) Owen Correspondence, xviii, 412.
(10) Letter from Charlesworth to James Pearce dated York, 29 April 1848, BRSMG, Geology File PEA 2.
(11) Joint report by Lyell and Forbes, in Forbes' handwriting, dated July 1848. Royal Society RR 1.161.
(12) Mantell, Gideon. Letter, 27 July 1849. Mantell family papers. MS Papers 83: folder 101. Alexander Turnbull Library, National Library of New Zealand, Wellington, New Zealand.

APPENDIX 2

List of specimens of Belemnotheutis *in the Pearce Collection, Bristol City Museum, ordered according to their numbers in Pearce's catalogue. All these specimens except the last three are catalogued in the Pearce MS catalogue as* Belemnoteuthis antiquus *Pearce, from 'Oxford Clay and Kelloway Rock'* (sic), *the locality being given as 'Nr. Chr. Malford'. For specimens denoted with an asterisk the original MS Pearce labels have the spelling* Belemnotheutis, *corrected to* Belemnoteuthis. *Pearce Catalogue numbers are bracketed.*

Ca5242 (160*). Small complete individual, 132 mm long. Pearce note reads '*perfect specimen* showing the capsule with its chambers, muscular mantle, ink bag, arms & hooks in situ &c it is remarkable that it has lost none of its external surface'. Figd Pearce 1847, plate 15, natural size. Acquired after the Geological Society paper was read, see Pearce (1847, p. 77).
Ca5240 (160A*). Complete specimen. Pearce note reads 'Specimen remarkable for a series of suckers on the inside of each of the arms. It also shows the arms with their hooks exceedingly perfect, the bodies surrounding the eyes, the muscular portion or body and its interior & the perfect capsule with its chambers.' Figd Pearce 1847, plate 16, reversed, and reduced to ×0·84. A piece in the middle of the phragmocone lost since figure. Acquired after the Geological Society paper was read, see Pearce (1847, p. 77). Lectotype here designated.
Cd21 (160B). Rectangular with corner missing, diagonal crack. Complete specimen about 175 mm long. Ink sac and duct. Arms (? 6 or 7) present as hooks only, no tissue preserved. Pearce's note for this group is 'Specimens showing the whole animal with its arms hooks &c remarkably fine, ink bag, muscular mantle, capsule &c'.
Cd22*a* (160B*). On tablet with Cd22*b*, Cd23*a*, Cd23*b*. Phragmocone (apex missing), 'body', ink sac (disintegrating, leaving impression). Possible broken and displaced pieces of pro-ostracum. Preserved length 193 mm, max. width 52 mm. For Pearce's note see Cd21.
Cd22*b* (160B*). Arm crown, with soft tissue and hooks. At least 6 arms. For Pearce's note see Cd21.
Cd23*a* (160B). Rectangular slab with corner detached. On tablet with Cd22*a*, Cd22*b*. Counterpart of Cd22*a*.
Cd23*b* (160B). Anterior part of body, confused, with parts of 2 arms, some hooks present. Possibly the counterpart of Cd22*b*.
Cd19 (160C*). Phragmocone (apex missing), mantle, ink sac and duct. A narrower white area in front of the mantle, fragmentary arms with scattered hooks. Pearce catalogue has 'Specimens well preserved & nearly entire showing the ink bag with its *duct*'.
Cd20 (160C*). Complete specimen 164 mm long. Ink sac, arms with hooks present. For remarks in the catalogue see entry for Cd19.
Cd18*a–b* (160D). Parallel-sided slab with phragmocone and mantle, dorsal view. Phragmocone shows groove and ridges. Counterpart of anterior half only. Preserved length 148 mm. Pearce catalogue has 'Entire specimen excepting its arms, remarkable for feathery processes passing off from the upper part of the body, and these are studded with little black pointed bodies'. The 'feathery processes' refer to muscular tissue in the neck region (see p. 291). It is not clear what the 'black ... bodies' are.
Cd15 (160E). A nondescript specimen, preserved length 117 mm, excluding possible small fragments of arms. Part of the mantle visible in centre. Neither phragmocone nor ink sac is clearly visible. Pearce's note for the specimens catalogued under the number 160E reads: 'A series of specimens of every part of the animal illustrating its different parts.'
Cd16 (160E). Rectangular slab, on black tablet, with phragmocone (apex missing) and mantle. Preserved length 128 mm.
Cd17 (160E). Rectangular slab on black tablet. Displaced mantle fragments, ink sac. Preserved length 125 mm. Counterpart of Cd16.
Cd24 (160E). On tablet with Cd25. Phragmocone and posterior part of the mantle. Dorsal side.
Cd25 (160E). The counterpart of Cd24.

Cd27 (160E). Part of phragmocone, and ?part of ink sac, displaced.
Cd26 (160E). Anterior end of phragmocone and part of mantle of a small individual. Preserved length 70 mm.
Cb3966 (160E). Complete phragmocone, length 86 mm, width at anterior end 46 mm. Dorsal side, shows apical groove and ridges.
Cb3967 (160E). Complete phragmocone, length 64 mm, width at anterior end 37 mm.
Cb3968 (160E). Phragmocone (apex missing), posterior part of 'body'. Preserved length 131 mm. Broken and jumbled.
Cb3969 (160E). Phragmocone, disturbed pieces of the mantle, fragment of ink sac. Preserved length 113 mm. Dorsal side.
Cb3970 (160E). On a black tablet with Cb3971. Phragmocone. Length 94 mm, width at anterior end 56 mm.
Cb3971 (160E). Phragmocone. Length along mid-like 72 mm, width at anterior end 49 mm.
Cb3972 (160F). Phragmocone, much larger than the others. Probably dorsal side. Length 303 mm, broken apex; estimated 310 mm when complete. However it may be made up from two different individuals; if so, the estimated total length is meaningless.
Cb3973 (160G). On black tablet with Cb3974–6. Apical part of a phragmocone. Pearce note reads 'A series of the capsules with their chambers, uncrushed, showing the natural shape, the siphunculus, and the thickness of the capsule, together with its radiated structure.'
Cb3974 (160G). Apical part of a phragmocone. For Pearce note see Cb3973.
Cb3975 (160G). Phragmocone, not flattened, preserved in calcareous mudstone. Possibly not *Belemnotheutis*. For Pearce note see Cb3973.
Cb3976 (160G). As last.
Cb3977 (–). Phragmocone, in a poor state. Figd Mantell, 1848, pp. 175–176, plate 13, fig. 1.
Cb7661 (–). Much disturbed specimen with phragmocone, mantle, ink sac, arms. Lacks label in Pearce's hand; later Museum label attributes it to Pearce coll. Figd Allison, 1988, figs 2B, 3–4.
Cb7662 (–). Part of mantle and ink sac. Lacks label in Pearce's hand; later Museum label attributes it to Pearce Colln.